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Kleptoparasitic melees - modelling food stealing featuring contests with multiple individuals

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Abstract. Kleptoparasitism is the stealing of food by one animal from another. This has been modelled in various ways before, but all previous models have only allowed contests between two individuals. We investigate a model of kleptoparasitism where individuals are allowed to fight in groups of more than two, as often occurs in real populations. We find the equilibrium distribution of the population amongst various behavioural states, conditional upon the strategies played and environmental parameters, and then find evolutionarily stable challenging strategies. We find that there is always at least one ESS, but sometimes there are two or more, and discuss the circumstances when particular ESSs occur, and when there are likely to be multiple ESSs.

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1. Introduction

A problem shared by all animals is finding a sufficient amount of food, and discovering food items can involve a significant period of searching. Whilst foraging, an individual can come into contact with conspecifics also seeking food, and it may discover an individual already in possession of a food item. It may then attempt to steal the food item; such stealing of items of food by one animal from another is termed kleptoparasitism (Rothschild and Clay 1952), and is common amongst many types of animals for example insects (Jeanne 1972), fish (Grimm and Klinge 1996) and mammals (Kruuk 1972). It is perhaps most common in birds (see Brockmann and Barnard 1979 for a review), and especially seabirds (Steele and Hockey 1995, Triplet et al. 1999, Spear et al. 1999).

However, the gain from attempting to steal a food item must be weighed against the costs e.g. time wasted, risk of injury involved in a contest. The individual must then make a choice whether to steal or not, based upon such rewards or costs; this provides an ideal scenario for the application of game theory (Maynard Smith, 1982). A significant body of literature using game theoretic models to investigate kleptoparasitic behavior in nature has been built up (e.g. Barnard and Sibly 1981; Stillmann et al. 1997; Broom and Ruxton 1998; Ruxton and Broom 1999; Broom and Ruxton 2003). The original model of Broom and Ruxton (1998) has been developed in a variety of ways in recent papers. For instance Luther and Broom (2004) showed that key dynamic assumptions of the model were correct, Broom et

al. (2004) developed the game by allowing handling birds to surrender food items and varying the success probability of the contestants, Broom and Rychtář (2007) analysed the models using adaptive dynamics for the first time, and Luther et al. (2007) considered two groups of birds, kleptoparasites and those which only foraged. However in each of these papers, fights were limited to two contestants only. In all of these earlier models, the key ingredient was this contest over food between the two animals, and where the different models gave different results, it was often because the nature of these contests changed from one scenario to another.

If an individual came across a contest for food already in progress, it was not allowed to intervene. This is not always reasonable, and it has been observed (e.g. Steele and Hockey, 1995) that large numbers of birds can fight over the same piece of food. Such groups can be particularly visible compared to smaller contests, and so such multiple contests may be very common. In this paper we explore this situation by allowing challenges to groups contesting a food item, and individuals have to decide whether to challenge any given sized group.

We find the equilibrium distribution of the population conditional on the strategies employed by the population members and find conditions when it is worth challenging a group in a given situation; this is more complicated than in the previous models (e.g. Broom and Ruxton, 1998; Broom et al., 2004) where only single individuals could be challenged. Every individual can choose what size groups it is prepared to challenge. We investigate how

large a group is worth challenging and the distribution of contest sizes in the population. We show that the only sensible strategies are to challenge groups up to a certain maximum size, and not to challenge larger groups. In particular we look for what parameter values such strategies are Evolutionarily Stable Strategies (ESSs). We show that there is always at least one ESS in every case, but that there can be two or more ESSs, sometimes many.

2. The Model

Individuals are either searchers, handlers, or involved in fights. Such kleptoparasitic contests can involve fights in groups of size i, for general $i \geq 2$. Searchers are allowed to challenge groups already involved in a contest, thus increasing the number of contestants by one. Note that in the original model of Broom & Ruxton (1998) individuals were only allowed to fight in groups of size two.

Transitions between the states occur according to a continuous time Markov chain, so every possible transition is associated with a single rate. Food is found at rate $\nu_f f$, and is handled at rate $1/t_h$. All fights, irrespective of the size of the groups, end at rate $1/t_c$, where t_c is the expected duration of a contest. We assume this for the sake of simplicity; in particular the calculations for Section 3.1 relating to optimal strategies would be greatly complicated if contest time varied. In Broom and Ruxton (1998) and subsequent papers, where all such contests contained two individuals, this average fighting time t_c was written as $t_a/2$. The proportion of searchers

	Meaning
$\nu_f f$	the rate at which food items are found
$1/t_h$	the rate at which food items are handled
$1/t_c$	the rate at which fights are resolved
μ_1	the rate at which handlers are found
μ_i	the rate at which groups of i fighters are found
s	the proportion of searchers in the population
h	the proportion of handlers in the population
f_i	the proportion of individuals in groups of size i
g_i	$g_i = f_i/i$, the relative density of groups of i individuals; $g_1 = h$
p_1	the probability a handler is challenged if found
p_i	the probability a group of i fighters is challenged if found
$\mathbf{p}$	the challenging strategy, $\mathbf{p}$= $(p_1, p_2, p_3, \ldots)$
V_k	the strategy to challenge groups of size $< k$ only
π_i	the probability of becoming a handler when currently in G_i
ρ_i	the probability that a new individuals joins G_i
X_k	any value X if all individuals play V_k
	(e.g. g_i becomes $g_{i,k}$)

Table 1. A summary of model parameters (top section) and notation (bottom section).

and handlers in the population are labelled s and h respectively. In Broom and Ruxton (1998) the density of searchers and handlers S and and H were considered, so that $s = S/P$ and $h = H/P$. The proportion of individuals involved in a contest of size i is labelled f_i ($f_2 = A/P$ in e.g. Broom et al., 2004), and the consequent ratio of the number of groups of size i to the population size is $g_i = f_i/i$. Searchers find groups of size i fighting over

food at rate $\mu_i g_i$ (so that the rate of finding a handler is $\mu_1 h$, equivalent to $\nu_h H = \nu_h h P$ in Broom and Ruxton (1998), and thus $P\mu_1 = \mu_h$). When a searcher sees a group of size i, it challenges with probability p_i (so the probability of challenging a handler is p_1). These probabilities may be fixed properties of the population, or be potentially different for different individuals. We will be particularly interested in the optimal values of p_i if all possibilities are allowed in the population. When contests end each group member is equally likely to be the winner, and emerge as a handler, all others becoming searchers. The parameters of the model are summarised in Table 1 and the transitions are shown in Figure 1.

The transitions translate into the following system of differential equations for s, h and g_i.

$$\frac{ds}{dt} = \frac{h}{t_h} - \nu_f f s + \frac{1}{t_c}\sum_{i=2}^{\infty}(i-1)g_i - \mu_1 p_1 s h - s\sum_{i=2}^{\infty}\mu_i p_i g_i \tag{1}$$

$$\frac{dh}{dt} = \nu_f f s - \frac{h}{t_h} - \mu_1 p_1 s h + \frac{1}{t_c}\sum_{i=2}^{\infty} g_i \tag{2}$$

$$\frac{dg_i}{dt} = \mu_{i-1} s g_{i-1} p_{i-1} - \frac{1}{t_c} g_i - g_i \mu_i s p_i \qquad i = 2, 3, \ldots \tag{3}$$

As shown in the Appendix, the equilibrium solutions are given by

$$h = t_h \nu_f f s \tag{4}$$

$$g_2 = \frac{t_c \mu_1 p_1 t_h \nu_f f s^2}{1 + t_c \mu_2 p_2 s} \tag{5}$$

$$g_i = g_2 \prod_{j=3}^{i}\left(\frac{\mu_{j-1} p_{j-1} s}{\mu_j p_j s + 1/t_c}\right) \tag{6}$$

where s is a solution of

$$1 = s(1 + t_h \nu_f f) + t_h \nu_f f s \sum_{i=2}^{\infty} i \prod_{j=2}^{i}\left(\frac{t_c \mu_{j-1} p_{j-1} s}{t_c \mu_j p_j s + 1}\right) \tag{7}$$

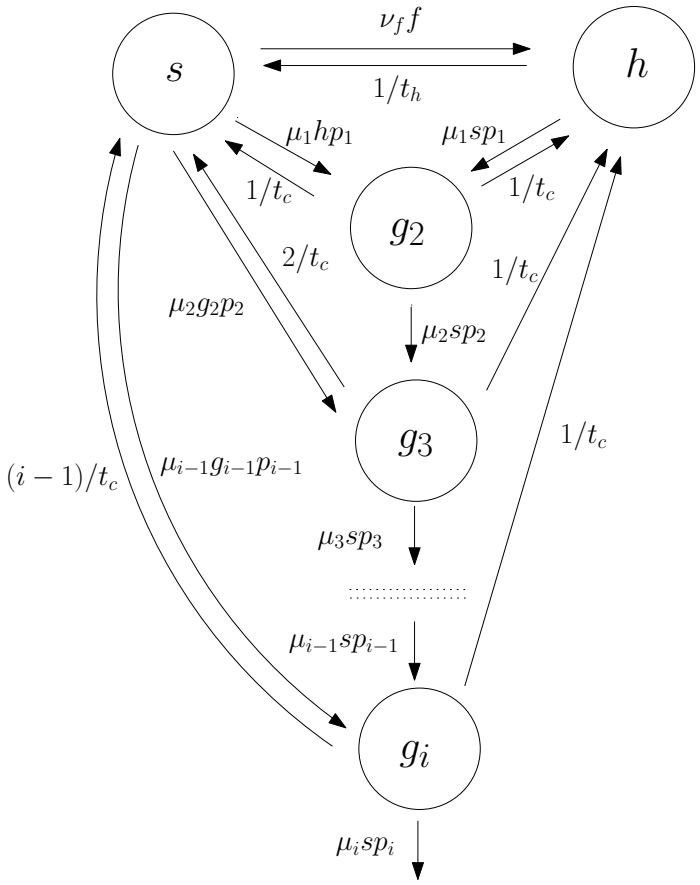

Fig. 1. Schematic description of the model.

Since the right hand side of (**??**) is monotone in s, it is clear that there is always a unique solution of (**??**). Also note that if $p_1 > 0$ and $p_i = 0$, for all $i > 1$, then (**??**) recovers the original Broom & Ruxton (1998) model.

As further shown in the Appendix, the expected time to become a handler for a searching individual who uses a strategy $\mathbf{q} = (q_1, q_2, \ldots)$ in the population where everybody else uses a strategy $\mathbf{p} = (p_1, p_2, \ldots)$ is

$$T_S = \frac{1 + t_c \sum_{i=1}^{\infty} \mu_i g_i q_i}{\nu_f f + \sum_{i=1}^{\infty} \mu_i g_i q_i \pi_{i+1}}. \tag{8}$$

where

$$\pi_i = \frac{1}{i} - \sum_{l=i}^{\infty} \frac{1}{l(l+1)} \prod_{j=i}^{l} \left(\frac{t_c \mu_j p_j s}{1 + t_c \mu_j p_j s} \right) \tag{9}$$

is the probability to become a handler when currently in the group of size i.

Note that T_S can be considered as the sole indicator of the fitness of an individual: the shorter the time, the higher the fitness. The fitness of an individual is in reality the rate at which it consumes food. It can consume food (at average rate $1/t_h$) if and only if it is the handling state, so that an individual's mean consumption rate is h/t_h (Broom and Ruxton, 1998). Any individual goes through searching periods of length T_S when it is either looking for a food item or fighting for an item as a challenger and through handling and defending periods where it is either handling or defending the food item against challenger(s). Varying an individual's own challenging strategy has an effect on the duration of the searching period. However, since in this paper we assume that the handler has to defend the food whenever challenged and no individual can give up the fight at any moment, an individual cannot vary the time it spends in the handling period once it begins handling (nevertheless, the length of the period depends on the behavior of others). Consequently, to maximize the proportion of time spent handling h, and thus its fitness, the individual should try to minimize T_S.

3. Evolutionarily Stable Strategies

We now consider the various situations that an individual may face, and what the best strategy is in each case. In particular, if a group of i individuals involved in a contest is observed, should a bird challenge or not (i.e. what should its value of p_i be)? We shall assume that all other individuals in the population play the strategy $\mathbf{p} = (p_1, p_2, \ldots)$ and we consider a mutant individual playing $\mathbf{q} = (q_1, q_2, \ldots)$. We find what ESSs are possible, and then conditions for each of them to actually be ESSs.

3.1. Possible ESSs

Here we show that any ESS must be a strategy V_k which challenges any groups of size less than k and no other. When faced with the opportunity to challenge a group of size i the best option is the one which has the least expected time to become a handler. If one does not challenge, the expected time is T_S. If one challenges, the Markov property guarantees that the contest takes an average time of t_c no matter whether and how many challengers join the group. Thus the expected time taken for an individual to become a handler when joining such a contest already containing i individuals is

$$t_c + 0 \times \pi_{i+1} + T_S \times (1 - \pi_{i+1})$$

Comparing T_S with the above shows that an individual should joint a contest if

$$\frac{\pi_{i+1}}{t_c} > \frac{1}{T_S}. \tag{10}$$

Thus, by (**??**), $q_i = 1$ is optimal if

$$\pi_{i+1} - t_c \nu_f f + t_c \sum_{j=1}^{\infty} \mu_j g_j q_j (\pi_{i+1} - \pi_{j+1}) > 0. \tag{11}$$

Otherwise, $q_i = 0$ is optimal.

The left-hand term of (**??**) is clearly decreasing with i, so that for any internally consistent set of q_is (i.e. each q_j is optimal in conjunction with $\mathbf{q}= (q_1, q_2, q_3, \ldots)$), optimal invading strategies must be of the form $q_i = 1$, for $i < k$ and $q_i = 0$, for $i \geq k$, for some constant k; i.e. groups up to a certain size only should be challenged.

We have shown that if any strategy can invade residents playing $\mathbf{p}$, a strategy V_k, for some k, can invade. What is the "best" of such potentially invading strategies will depend upon the values of the p_is, while although they do not appear in (**??**) explicitly, they do implicitly since the g_is and π_is are functions of them. Note also that any strategy $\mathbf{p}$ which is not of the form V_k must be invadable, since we can consider a 'mutant' which plays $\mathbf{p}$ exactly. It clearly performs equally well to the resident population, but above we have shown that there is a better mutant, which hence must invade. We can thus confine our attentions to the strategies V_k.

For a population all playing V_k, the maximum group size is k, occurring when a group of size $k-1$ is challenged. We can use (**??**) to find the value of s, and then (**??**), (**??**), (**??**), and (**??**) to give the values of h, g_2, g_i, and π_i. Each of these will depend upon the value of k and we thus label the values of s, h, g_i and π_i for a population playing strategy V_k as $s_k, h_k, g_{i,k}$ and $\pi_{i,k}$ respectively.

$\nu_f f$	0.01	0.11	0.21	0.31	0.41	0.51	0.61	0.71	1.21	2.51
s_7	963	749	640	568	515	474	441	414	321	213
h_7	9.63	82	134	176	211	242	269	294	389	535
$g_{2,7}$	4.73	35	52	64	72	78	82	86	95	94
$g_{3,7}$	2.32	15	20	23	24	25	25	25	23	16
$g_{4,7}$	1.14	6.47	7.97	8.36	8.31	8.06	7.72	7.35	5.59	2.90
$g_{5,7}$	0.56	2.77	3.11	3.03	2.82	2.59	2.36	2.15	1.36	0.509
$g_{6,7}$	0.27	1.19	1.21	1.10	0.960	0.83	0.72	0.63	0.03	0.01
$g_{7,7}$	0.26	0.89	0.78	0.62	0.5	0.4	0.32	0.26	0.11	0.02

Table 2. Proportion of individuals and groups (times 10^3) for strategy V_7 as $\nu_f f$ varies. Other parameter values are $t_h = 1, t_c = 1, \mu_i = \mu_1 = 1$. Note that the proportion of individuals involved in a fight in the group of size i is ig_i and not g_i.

For illustration we give a numerical example; the densities of the various group sizes for the example population V_7 are shown in Table **??**. As the rate of finding food increases, the densities of searchers declines, the density of handlers increases, and the density of groups of each size first increases and then declines.

3.2. Conditions for strategy V_k to be an ESS.

Consider a population of individuals playing V_k. When can an individual playing V_l invade?

If $l > k$ then groups of resident individuals form only up to size k, so that our individual may challenge such a group, but will never get the opportunity to challenge larger groups. Thus the strategy indicated for encounters

with such groups is irrelevant, and the payoff to any strategy V_l, $l > k$ is identical, and so equal to the payoff of V_{k+1}.

Now suppose that $l < k$. V_l invades V_k when T_S is smaller for the invader than for the resident. By (**??**), this happens if

$$\frac{1 + t_c \sum_{i=1}^{l-1} \mu_i g_{i,k}}{\nu_f f + \sum_{i=1}^{l-1} \mu_i g_{i,k} \pi_{i+1,k}} < \frac{1 + t_c \sum_{i=1}^{k-1} \mu_i g_{i,k}}{\nu_f f + \sum_{i=1}^{k-1} \mu_i g_{i,k} \pi_{i+1,k}}$$

which is equivalent to

$$\sum_{i=l}^{k-1} \mu_i g_{i,k} \left(\nu_f f t_c - \pi_{i+1,k} + t_c \sum_{j=1}^{l-1} \mu_j g_{j,k} (\pi_{j+1,k} - \pi_{i+1,k}) \right) > 0 \qquad (12)$$

The term in brackets in (**??**) increases with both l and i. For $l = k - 1$ there is just a single term, and if this is negative then invasion does not occur. If $l < k - 1$, then the expression consists of the sum of several of these terms, all smaller than the $i = l = k - 1$ term, so that invasion of V_l cannot occur for $l < k - 1$ if it does not occur for V_{k-1}.

A strategy V_k is thus an ESS if and only if it can resist invasion by both V_{k-1} and V_{k+1} for $k \geq 2$ (V_1 must resist invasion only from V_2). This is equivalent to saying that in a population of V_k individuals the optimal strategy when encountering a group of size $k - 1$ is to challenge ($q_{k-1} = 1$) and the optimal strategy against a group of size k is not to challenge ($q_k = 0$). By (**??**), this is equivalent to

$$t_c \nu_f f > \frac{1}{k+1} - t_c \sum_{i=1}^{k-1} \mu_i g_{i,k} \left(\pi_{i+1,k} - \frac{1}{k+1} \right) \qquad (13)$$

$$t_c \nu_f f < \frac{1}{k} - t_c \sum_{i=1}^{k-1} \mu_i g_{i,k} \left(\pi_{i+1,k} - \frac{1}{k} \right), \qquad (14)$$

since, in a population of V_k individuals, $\pi_{k,k} = 1/k$ and $\pi_{k+1,k} = 1/(k+1)$ for any mutant that challenged a group of size k; note that $\pi_{i,k} < \frac{1}{i}$ for $i < k$.

Notice that the right hand side of (**??**) is always smaller then the right hand side of (**??**). Thus since (**??**) is satisfied for sufficiently large $t_c\nu_f f$, there is an interval of values of $t_c\nu_f f$ for which V_k is an ESS.

It follows directly from (**??**) that V_1 cannot be invaded by V_2 if and only if

$$t_c\nu_f f > \frac{1}{2}.$$

It is easy to see from (**??**) and the fact that $1/k \leq \pi_{i,k} < 1/i$ for $i < k$, $t_c\nu_f f < \frac{1}{2}$ is a necessary condition for V_k to be an ESS when $k > 1$.

3.3. Overlapping regions and multiple ESSs

We start to consider the possibility of multiple ESSs with a range of numerical examples. Table **??** shows the different group sizes for the ESS strategy for varying $\nu_f f$ with other parameters fixed (note that for $\nu_f f = 0.31$ there are two ESSs and both of these are given).

Figure **??** shows the range of values of $\nu_f f$ for which each of the strategies V_k are ESSs for $k = 1, 2, \ldots, 10$. We are particularly interested in the overlaps between the regions, when there are multiple ESSs.

Table **??** shows the range of $\nu_f f$ where specific V_k are ESSs for different values of P, following on from Figure **??**. The cases with multiple ESSs required the combination of little food and large encounter rates, leading to

$\nu_f f$	0.11	0.21	0.31	0.31	0.41	0.51
ESS	k=7	k=4	k=3	k=2	k=2	k=1
s_k	0.749	0.644	0.577	0.596	0.540	0.662
h_k	0.082	0.135	0.179	0.185	0.221	0.338
$g_{2,k}$	0.035	0.053	0.065	0.110	0.119	0
$g_{3,k}$	0.015	0.021	0.038	0	0	0
$g_{4,k}$	0.006	0.013	0	0	0	0
$g_{5,k}$	0.003	0	0	0	0	0
$g_{6,k}$	0.001	0	0	0	0	0
$g_{7,k}$	0.0009	0	0	0	0	0

Table 3. Group sizes for ESSs as $\nu_f f$ varies, other parameter values: $t_h = 1, t_c = 1, \mu_i = \mu_1 = 1$.

intense contests and very little consumption, which of course is not realistic. However, for more realistic encounter rates, there will be overlaps, but perhaps not more than two or three ESSs for any given value of $\nu_f f$.

By comparing the right-hand side of (**??**) for V_k and the right-hand side of (**??**) for V_{k+1}, as we do in the Appendix, we see that there is an overlap between successive regions.

For small encounter rates $\mu_i \approx 0$ the conditions (**??**) and (**??**) reduce to

$$\frac{1}{k} > \nu_f f t_c > \frac{1}{k+1}$$

which means almost no overlaps between the ESSs. On the other hand, for extremely large μ_is, any fight effectively ends up as a fight between k individuals and thus $\pi_{i,k} \approx 1/k$ which means that the condition (**??**)

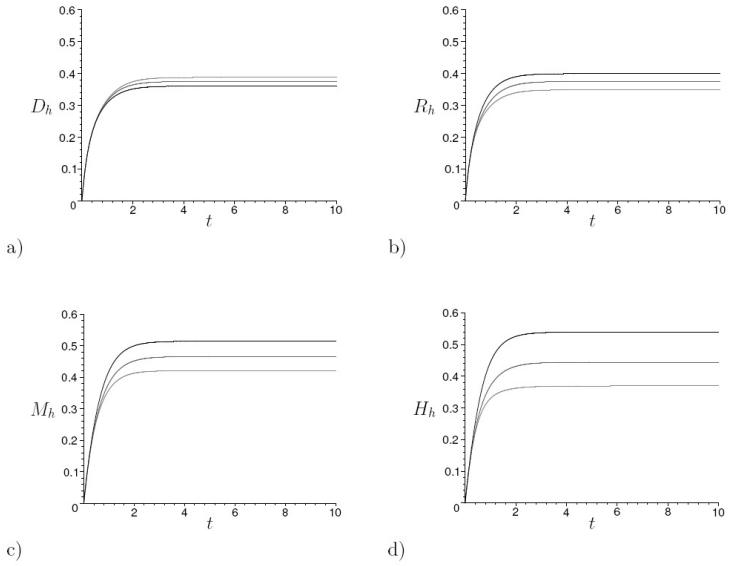

Fig. 2. Ranges of $\nu_f f$ for specific V_k to be ESS. a) $\mu_i = \mu_1 = 0.1$, b) $\mu_i = \mu_1 = 1$, c) $\mu_i = \mu_1 = 10$, d) $\mu_i = \mu_1 = 100$, e) $\mu_i = \mu_1 = 1000$. Other parameter values are $t_h = 1$ and $t_c = 1$.

becomes

$$\nu_f f t_c > 0$$

and so there are significant overlaps between a large number of strategies.

4. Discussion

Kleptoparasitic contests involving multiple competitors are common in nature (Steele and Hockey, 1995), but have not before now been modelled mathematically. In this paper we have developed the model of Broom and Ruxton (1998) to allow for such contests. In contrast to previous models (Broom and Ruxton, 1998; Broom and Rychtář, 2007) when a group of

k\ μ_i	0.1	1	10	100	1000
1	[.5,∞)	[.5,∞)	[.5,∞)	[.5,∞)	[.5,∞)
2	[.330, .500)	[.304,.500)	[.207, .500)	[.068, .500)	[.0100, .500)
3	[.246, .329]	[.220, .314]	[.149, .296]	[.053, .289]	[.0078, .286]
4	[.196, .245]	[.170, .222]	[.113, .194]	[.046, .184]	[.0077, .178]
5	[.163, .195]	[.137, .17]	[.089, .136]	[.039, .125]	[.0079, .118]
6	[.139, .162]	[.114, .136]	[.071, .101]	[.035, .087]	[.0080, .083]
7	[.121, .138]	[.098, .113]	[.058, .078]	[.03, .065]	[.0081, .061]
8	[.108, .12]	[.085, .097]	[.049, .062]	[.025, .05]	[.0080, .046]
9	[.097, .107]	[.075, .084]	[.041, .051]	[.023, .039]	[.0078, .036]
10	[.087, .096]	[.068, .074]	[.035, .042]	[.02, .032]	[.0075, .028]

Table 4. Ranges of $\nu_f f$ where specific V_k is an ESS with varying μ_i; other parameter values: $t_h = 1, t_c = 1$.

individuals contesting a food item is observed, then it is possible for the observer to join the contest in the hope of acquiring the food item. The chance of success will decrease with the number of other competitors, and we investigate a number of possible scenarios. For a defined challenging behaviour we find the equilibrium distribution of the sizes of the population density in each of the different categories of activity; there is a single equation for the density of searchers, from which all other densities can be found.

In particular we are interested in the possible strategies of individuals, and finding the best strategies under different conditions. We find ESSs for various parameter values. It is likely of course, that some of the parameter values will vary during the course of an individual's life, especially throughout the year. For example food availability is likely to be affected by seasonal

factors. Thus if individuals played only the fixed strategies that we mention here, they could be outcompeted by those with more flexible strategies. In common with earlier models (Broom and Ruxton, 1998; Luther and Broom, 2004; Broom et al., 2004), we assume that individuals rather have the ability to respond to certain cues to gauge the level of different parameters, and so be capable of adjusting between the different V_k over the course of a season. Provided individuals are capable of making this switch efficiently, then consideration of the ESSs for any fixed set of parameters is sufficient to find the correct behaviour. However if there is more than one ESS for a given parameter set, the history of the parameter values could play an important role in determining which solution would be chosen in practice. Thus it would be of interest to investigate such variable parameters.

It should be noted that strategies considered in the present paper are more complex here than in most previous models e.g. Broom et al. (2004). In this and related models, when a challenge is made (and resisted) then the contest duration is fixed, its real cost is determined by the level of foraging success that could be expected when not in the contest and the benefit of being in the contest is fixed as well (often, the contest is won 50% of the time). In our model further individuals may challenge groups and this makes the evaluation of the benefits of entering the contest more complex. It is for this reason that we see many possible strategies, and that multiple ESSs can occur for a given set of parameters.

Earlier models did come up with interesting predictions based upon different assumptions to the model in the current paper. For instance Broom et al (2004) allowed individuals to decline to resist attacks, and the strategy of attacking but never resisting, termed Marauder, was shown to be stable for a large range of parameter values. Such short contests with the defender offering no resistance have been discovered in real populations, for example in wading birds (Stillman et al., 1997). The model of Broom and Ruxton (2003) allowed individuals to feed on items which had constant handling time, and to make choices based upon the length of handling time remaining. Optimal choices were found which depended upon the critical remaining handling time, so that items which were consumed continuously were challenged for only if there was sufficient remaining handling time, but items which were consumed at once at the end of the handling time, as here, were challenged for only if the remaining time was sufficiently short.

We show that when individuals may or may not challenge groups of any size, the only viable strategies involve only challenging groups up to a certain size, and always challenging these. Thus there are an infinite number of possible strategies. Individuals display varying levels of "Hawkish" behaviour, rather than just Hawk or Dove, or more appropriately (since all individuals resist attacks) Hawk or Retaliator (Maynard Smith, 1982). We have derived conditions as functions of our parameters for different strategies to be ESSs. It should be noted that since the rate that the population acquires food (its uptake rate) is proportional to the proportion of handlers

h_k, it decreases with the size of group individuals are prepared to challenge. Its largest value is given by the classical result from Holling (1959) when no individuals challenge, but only forage, and falls away sharply if individuals challenge handlers only (Broom and Ruxton, 1998, and see also Ruxton and Moody, 1997, when all individuals were compelled to fight).

We have found that there is always at least one ESS. As we vary the food density we can see how the pattern of ESSs changes. From high food availability we move from never challenging being an ESS, to challenging only handlers, to challenging handlers and fighting pairs and so on. As the availability of food declines, individuals are willing to challenge larger and larger groups. As the population moves from one situation to the next, there is an overlap region where both strategies are ESSs (except when going from no challenges to challenging handlers only). If the encounter rate is small, the overlap is small, and in most scenarios there will be a single ESS. However, for larger encounter rates this overlap can become substantial; in fact it can be sufficiently large for there to be three or more ESSs. It should be noted that these situations only occur for very (generally unrealistically) large encounter rates, when competition for food is intense. They are theoretically possible however, and situations where there are three ESSs are plausible.

In Broom and Ruxton (1998) and subsequent models, this overlap has not previously been observed, because only handlers could be challenged, and there is no overlap between the no challenge (V_1) and only challenge

handlers (V_2) regions. It is possible to have two ESSs simultaneously, because an individual chooses to challenge a group of given size if and only if the rate that it finds food by not challenging is sufficiently poor. Unless we are considering the rate of finding food of an individual which does not challenge handlers (which is always $\nu_f f$), this rate is reduced the more others in the population are prepared to challenge, and so it can be best to challenge if all others are going to challenge, and not challenge if they are all not going to challenge. Situations with more than one ESS have been found in other models, often for similar reasons (that the strategies of others not involved in a particular contest affects this background uptake rate) but never a potentially unlimited number of ESSs as in the current paper.

The model developed in this paper predicts significantly different behaviour to those allowed in previous models (Broom et al., 2004; Broom and Rychtář, 2007; Luther et al., 2007) in particular when food is quite rare and/or encounter rates are large. When food is plentiful it pays nobody to fight, and the extra possibility of multiple contests adds nothing. If the encounter rates are small, individuals are unlikely to chance upon competing groups; thus although theoretically their strategy might be to challenge groups of size seven or less, they will rarely in practice experience such a situation. Our model is also only realistic if individuals are foraging in close proximity and it takes some time to handle the food. For instance Shealer and Spendelow (2002) examined a real situation where foragers travelled significant distances to find food, but had to return to the nest site to feed

their young, and kleptoparasites waited near the nest to try to steal. Multiple fights would be possible in this situation, but the symmetry of our model would be lost, as there would be at least two distinct types of individual in the population, as modelled in Luther et al. (2007).

In this paper we have extended the original and simplest of a series of recent game theoretic models of kleptoparasitic behaviour, so that to allow for multiple contests we have re-introduced some of the original simplifications of this model. It would be of interest to develop the current model with some of the more complex features of later models. For instance in Broom et al. (2004) individuals did not have to resist challenges, and handlers had a different probability of success to subsequent challengers.

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6. Appendix

6.1. Evaluating the proportions at the equilibrium

The solutions of the system of differential equations (**??**), (**??**), (**??**) tend to equilibrium exponentially fast (see e.g. Luther & Broom, 2004). Hence, the time derivatives can be considered 0 and by labeling the following summations

$$F_T = \sum_{i=2}^{\infty} i g_i$$

$$G_T = \sum_{i=2}^{\infty} g_i$$
$$G_S = \sum_{i=2}^{\infty} \mu_i p_i g_i$$

we obtain

$$0 = \frac{h}{t_h} - \nu_f f s + \frac{1}{t_c}(F_T - G_T) - \mu_1 p_1 s h - s G_S \tag{15}$$
$$0 = \nu_f f s - \frac{h}{t_h} - \mu_1 p_1 s h + \frac{1}{t_c} G_T \tag{16}$$
$$0 = \mu_1 s h p_1 - g_2 \left(\frac{1}{t_c} + \mu_2 s p_2 \right) \tag{17}$$
$$0 = (\mu_{i-1} s p_{i-1}) g_{i-1} - \left(\frac{1}{t_c} + \mu_i s p_i \right) g_i \qquad i = 3, 4, \ldots \tag{18}$$

Equation (**??**) rearranges to give

$$g_i = \frac{\mu_{i-1} p_{i-1} s}{\mu_i p_i s + 1/t_c} g_{i-1} = g_2 \prod_{j=3}^{i} \left(\frac{\mu_{j-1} p_{j-1} s}{\mu_j p_j s + 1/t_c} \right)$$

This in turn gives

$$F_T = g_2 \sum_{i=2}^{\infty} i \prod_{j=3}^{i} \left(\frac{\mu_{j-1} p_{j-1} s}{\mu_j p_j s + 1/t_c} \right)$$
$$G_T = g_2 \sum_{i=2}^{\infty} \prod_{j=3}^{i} \left(\frac{\mu_{j-1} p_{j-1} s}{\mu_j p_j s + 1/t_c} \right)$$
$$G_S = g_2 \sum_{i=2}^{\infty} \mu_i p_i \prod_{j=3}^{i} \left(\frac{\mu_{j-1} p_{j-1} s}{\mu_j p_j s + 1/t_c} \right)$$

We now have the system completely expressed in terms of known parameters, assuming at this stage that the values of the p_is are known, and the three unknowns s, h and g_2. We now proceed to find expressions for each of s, h and g_2.

Equation (**??**) implies that

$$\sum_{i=3}^{\infty} g_i + \sum_{i=3}^{\infty} t_c \mu_i p_i s g_i = \sum_{i=2}^{\infty} t_c \mu_i p_i s g_i$$

and hence

$$G_T = \sum_{i=2}^{\infty} g_i = g_2 + t_c \mu_2 p_2 s g_2 = (1 + t_c \mu_2 p_2 s) g_2.$$

From (**??**) we also get, for any $k > i + 1$,

$$\begin{aligned} t_c \mu_i p_i s g_i &= (1 + t_c \mu_{h_{(i+1)}} p_{i+1} s) g_{i+1} \\ &= \sum_{j=i+1}^{k} g_j + t_c \mu_{hk} p_k s g_k = \sum_{j=i+1}^{\infty} g_j \end{aligned}$$

using the fact that $g_i \to 0$ as $i \to \infty$, and letting $k \to \infty$. Thus,

$$\begin{aligned} t_c s G_S = \sum_{i=2}^{\infty} t_c \mu_i p_i s g_i &= \sum_{i=2}^{\infty} \left(\sum_{j=i+1}^{\infty} g_j \right) \\ &= \sum_{i=2}^{\infty} (i-2) g_i = F_T - 2G_T \end{aligned}$$

and so

$$F_T - t_c s G_S = 2G_T = 2(1 + t_c \mu_2 p_2 s) g_2 \tag{19}$$

From (**??**) it is clear that equations (**??**), (**??**) and (**??**) multiplied by two add to zero and so there are really only two equations here. The third equation for our three unknowns comes from the fact that every individual is in exactly one state, so that

$$s + h + \sum_{i=2}^{\infty} f_i = s + h + F_T = 1 \tag{20}$$

Equations (**??**), (**??**) and (**??**) yield

$$h = t_h \nu_f f s. \tag{21}$$

This now means, using (**??**), that

$$g_2 = \frac{t_c\mu_1 p_1 t_h \nu_f f s^2}{1 + t_c\mu_2 p_2 s} \tag{22}$$

We thus have every other density term $(h, g_2, g_3, \ldots)$ expressed as a function of s. Finally we obtain an equation for s by substitution into (**??**). This yields

$$\begin{aligned} 1 = s + h + F_T &= s(1 + t_h\nu_f f) + g_2 \sum_{i=2}^{\infty} i \prod_{j=3}^{i} \left(\frac{t_c\mu_{j-1}p_{j-1}s}{t_c\mu_j p_j s + 1} \right) \\ &= s(1 + t_h\nu_f f) + t_h\nu_f f s \sum_{i=2}^{\infty} i \prod_{j=2}^{i} \left(\frac{t_c\mu_{j-1}p_{j-1}s}{t_c\mu_j p_j s + 1} \right) \end{aligned}$$

6.2. Calculation of the searching time.

Let T_S be the expected time to become a handler for a searching individual who uses a strategy $\mathbf{q} = (q_1, q_2, \ldots)$ in the population where everybody else uses a strategy $\mathbf{p} = (p_1, p_2, \ldots)$ and let π_i denote the probability of becoming a handler at the end of the contest when presently in a group of size i. We shall first consider individuals which join a contest. The Markov property guarantees that contests end at rate $1/t_c$ irrespective of the size of the group or whether new individuals have challenged since our focal individual joined the group. Thus the expected time taken for an individual to become a handler when joining such a contest already containing i individuals is

$$t_c + 0 \times \pi_{i+1} + T_S \times (1 - \pi_{i+1})$$

where t_c is the fight time, $0 \times \pi_{i+1}$ relates to the case that the individual eventually wins the fight, and $T_S \times (1 - \pi_{i+1})$ relates to the case that it loses the fight and has to search again. Following on from this, the expected time

to become a handler from the searching position is

$$T_S = \frac{1}{\nu_f f + \sum_{i=1}^{\infty} \mu_i g_i q_i} + \frac{\nu_f f}{\nu_f f + \sum_{i=1}^{\infty} \mu_i g_i q_i} \cdot 0 + \frac{1}{\nu_f f + \sum_{i=1}^{\infty} \mu_i g_i q_i} \sum_{i=1}^{\infty} \mu_i g_i q_i \Big(t_c + \big(\pi_{i+1} \cdot 0 + (1 - \pi_{i+1}) T_S \big) \Big)$$

where the terms correspond to 1) the time needed to encounter something, 2) the probability of encountering a food item (times 0 as the food is already found), and finally 3) the probabilities of encountering a group of size i times the time needed to become a handler after such an encounter. Hence,

$$T_S = \frac{1 + t_c \sum_{i=1}^{\infty} \mu_i g_i q_i}{\nu_f f + \sum_{i=1}^{\infty} \mu_i g_i q_i \pi_{i+1}}. \tag{23}$$

6.3. Calculation of π_i.

Since π_i is the probability of becoming a handler when in a group of size i, clearly $\pi_1 = 1$. For groups of size at least two, the next event that occurs is either the resolution of a contest, so that all individuals have an equal chance of gaining the food, or a new individual joining a contest. A new individual joins with probability

$$\rho_i = \frac{\mu_i p_i s}{1/t_c + \mu_i p_i s} = \frac{t_c \mu_i p_i s}{1 + t_c \mu_i p_i s} \tag{24}$$

so that, for $i \geq 2$,

$$\pi_i = \frac{1}{i}(1 - \rho_i) + \rho_i \pi_{i+1}. \tag{25}$$

Note that it follows immediately from (**??**) that

$$\pi_{i+1} < \pi_i$$

since, trivially, $\pi_{i+1} < \frac{1}{i}$. From (**??**) we also obtain

$$\pi_i = \frac{1}{i}(1-\rho_i) + \rho_i\left(\frac{1}{i+1}(1-\rho_{i+1}) + \rho_{i+1}\pi_{i+2}\right) = \dots$$
$$= \frac{1}{i} - \sum_{l=i}^{\infty}\frac{1}{l(l+1)}\prod_{j=i}^{l}\rho_j = \frac{1}{i} - \sum_{l=i}^{\infty}\frac{1}{l(l+1)}\prod_{j=i}^{l}\frac{t_c\mu_i p_i s}{1+t_c\mu_i p_i s}$$

since $\prod_{j=i}^{l}\rho_j \to 0$ as $l \to \infty$.

We will now consider the overlaps between strategies V_k. From (**??**) - since for V_k, p_i takes value 1 for $i < k$ and 0 otherwise - it is clear that s_k decreases with k. This in turn means that h_k, by (**??**), $g_{2,k}$, by (**??**), and $g_{i,k}$, by (**??**), all decrease with k. The intuitively clear result that also $\pi_{i,k} > \pi_{i,k+1}$ for all $i = 2, \cdots$ and all $k = 2, \dots$ was checked numerically for a large range of parameter values, although we have been unable to prove this mathematically. Assuming this result we obtain

$$t_c\sum_{i=1}^{k-1}\mu_i g_{i,k}\left(\frac{1}{k+1} - \pi_{i+1,k}\right) < t_c\sum_{i=1}^{k}\mu_i g_{i,k+1}\left(\frac{1}{k+1} - \pi_{i+1,k+1}\right) \quad (26)$$

because the extra term for $i = k$ of the sum on the right hand side of the above inequality is 0 since $\pi_{k+1,k+1} = 1/(k+1)$. Consequently, there are always some parameter values such that $t_c\nu_f f$ lies between those two and thus there is always an overlap between V_k and V_{k+1}.